DRYOPTERIS DILATATA (HOFFM.) A. GRAY IN NORTH AMERICA

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Taxonomic authorities have differed widely in their interpretation of the species of *Dryopteris* in North America which resemble the old world *Dryopteris dilatata* (Hoffm.) A. Gray. Fernald (1) considered the fern that is found in the Appalachians north to Quebec and Labrador, and yet resembles *D. dilatata* superficially, to be a variety of *D. spinulosa* (O. F. Müll.) Watt, namely *D. spinulosa* var. *americana* (Fischer) Fernald, whereas Morton in Gleason (2), refers to this entity as *D. austriaca* (Jacq.) Woynar var. *austriaca*. There has been similar disagreement concerning the species found in Montana and Oregon north to Alaska, although Taylor (3) employs the latter designation for the common form in British Columbia.

In a recent article in Brittonia, Wagner and Hagenah (4) have suggested that not only are the eastern and western entities separate species, but that within the range of Gray's Manual, *D. spinulosa* var. *americana* should be further separated into two species. Some evidence for the latter separation is found from Walker (5) who reported that *D. spinulosa* var. *americana* (*D. campyloptera* (Kunze) Clarkson) from Vermont and also Quebec is tetraploid (4X) (x=41), whereas Wagner reports that ferns in Michigan previously referred to as var. *americana* are diploid. I am in full agreement with these cytological findings because last spring I studied 12 collections of var. *americana* from Jefferson Notch and Mt. Washington, New Hampshire collected by R. and A. Tryon and all were tetraploids (Tryon 5684, 5689-5700 June 25, 1961). In 1960, I studied 11 collections of var. *americana* from Mile 80, north of Sault Ste. Marie, Ontario and these were all normal diploids (2X) (B373-383 June 23, 1960).

However, I take strong exception to the authors' suggestion that the Lake Superior diploid cannot be identified with western *D. austriaca* var. *austriaca* although both are diploid. The cytological argument is quite circuitous. Walker

(5) has named the diploid species of *dilatata* of the old world, *D. assimilis* S. Walker, and has considered that morphologically and cytologically *D. maderensis* Alston is inseparable from *D. intermedia* (Muhl.) A. Gray. (There is normal meiotic pairing between the chromosomes of *maderensis* and *intermedia*). In the two hybrids studied from a cross between *D. maderensis* × *D. assimilis*, Walker (5) found that there was also normal pairing but that ca. 40% of the spores aborted. He concluded on the basis of chromosomal homologies that *intermedia* and *assimilis* represented the same ancestral genome. Walker further suggested that "morphological similarity between the Vancouver diploid and *D. assimilis* suggests that they represent the same genome and possibly the same species." This conclusion was fortified by the fact that the progeny of the cross of the Vancouver diploid with the United Kingdom tetraploid *dilatata* gave the same cytological picture as the cross *D. assimilis* (2X) × *D. dilatata* (4X) namely ca. 41 pairs and 41 single chromosomes in meiosis. Wagner and Hagenah (4) found one hybrid between the putative parents *D. intermedia* and the Lake Superior diploid and report that there is little or no chromosomal pairing between the genomes of this plant, although the number of cells studied and the number of clear meiotic plates analysed is not given. Accordingly, they contrast Walker's cross (two plants) of *D. maderensis=intermedia* × *D. assimilis* with their one hybrid of *D. intermedia* × Lake Superior diploid, and conclude that if *D. assimilis* is identical with the Vancouver diploid then the Vancouver diploid is unlike the Lake Superior diploid. However, as yet we have no *direct* comparisons between these diploids. What is needed are hybrids between (a) the Lake Superior diploid and the western diploid (b) the Lake Superior diploid and *D. assimilis* and (c) the Western diploid and *D. intermedia*. It should also be evident that many more plants should be studied cytologically before reaching sweeping conclusions from meiotic analysis of one or two plants, some of which are hybrids of putative parents.

Although a cytotaxonomist is apt to be impressed with the evidence presented by Walker (5) to consider *D. ma-*

derensis Alston and *D. intermedia* (Muhl.) A. Gray as conspecific, there has as yet been no adequate taxonomic treatment to substantiate this conclusion.

It would seem extremely hazardous to put too much emphasis on pairing in spite of its great usefulness in genome analysis. *D. intermedia* and *D. assimilis* are morphologically separable and yet show good pairing, hence would be one species using this latter criterion alone. In fact this would leave *D. assimilis* Walker, *D. maderensis* Alston, *D. austriaca* var. *austriaca* in British Columbia, and *D. intermedia* as being all the same ancestral genome and the same species on the basis of genome analysis. The Lake Superior diploid, however, which so closely resembles the British Columbia diploid in morphology, and *must* be closely related, is then considered to be an entirely different species merely on its pairing behaviour with *intermedia*.

Two pieces of cytogenetic evidence should be kept in mind to temper the use of the criterion of chromosome pairing. One is the finding in wheat that pairing is under genetic control and governed by the presence or absence of genes for synapsis (6). If this should prove to be true in *Dryopteris*, the basis of genome analysis would be invalidated. The other point may be related, and concerns races of *Asplenium trichomanes* in Ontario (7). These races are morphologically extremely similar and yet one is diploid and the other is tetraploid without multivalent pairing at meiosis. If the latter is an autotetraploid with four identical genomes as it appears on morphological grounds, then why are only bivalents formed? It would seem that the tetraploid has become effectively "diploidized." A similar situation to this was found to be present in *Pellaea ternifolia* which had both diploid and tetraploid sexual races which formed only bivalents at meiosis (8).

It should be stressed that all hybrids found in the wild are given parentage on the basis of their intermediate morphology between putative parents. The interesting plant (Wagner 9434) assigned to *D. "dilatata"* (Lake Superior diploid) × *D. intermedia* is described by Wagner and Hagenah (4) cursorily as an intermediate, and one has no

way of knowing whether it is the result of an average or typical Lake Superior diploid × an average or typical *intermedia*, or for that matter whether it could not be an atypical *intermedia* × an atypical *D. marginalis*. A further possibility is that this plant (Wagner 9434) is a hybrid of a glandular Lake Superior "*dilatata*" × *marginalis*, since the illustrations of the authors' look similar. The point is, that nothing is known of the characteristics of the parents except as they are represented in the hybrid. In this case, "the leaf form was intermediate" although "the previous year's leaves were green and persistent."

The morphological data given by Wagner and Hagenah (4) for the western diploid is extremely scanty. There is no mention of the number of specimens examined or where they might have been from. The findings are summarized in six lines and concern such variable features as petiole scales and leaf blade shape.

The authors (4) disregard the plant geographical evidence. One can assemble quite an impressive array of species in the Lake Superior basin that are of Cordilleran affinities. Stebbins (9) lists ten species found even further east in the Bruce Peninsula, Ontario, that may be considered Rocky Mountain types. Butters and Abbe (10) list four western American types in a table of 70 rare species found in Cook County, Minnesota. Among the ferns of the Lake Superior basin, *Cystopteris montana*, *Woodsia scopulina*, and *Cryptogramma crispa* are considered to have western affinities.

Accordingly, when the geographical, morphological and cytological evidence is reviewed critically, one can only conclude that the western diploid, *D. dilatata (D. assimilis)*, and the Lake Superior diploid, *D. dilatata (D. spinulosa* var. *americana)* have not as yet been shown to be distinct and separate species.

Concerning the eastern tetraploid, *D. campyloptera* Clarkson, Wagner and Hagenah (4) suggest that this might be an allotetraploid of *D. intermedia* × Lake Superior diploid. An alternative suggestion that it is an ancient autotetraploid of the Lake Superior diploid which in turn is a diploid "*D.*

dilatata" (D. assimilis) cannot be disregarded on the available evidence. *D. campyloptera* which now forms only bivalents could be analagous to the tetraploid race of *Asplenium trichomanes.*

One is confronted in *Dryopteris* with the larger problem of what is a species? Wagner is a proponent of biological species, but critical criteria for separating species are few in the *Dryopteris spinulosa* complex. All the species are apparently able to cross with one another, consequently this is of little use as a limiting criterion, although much used for genome analysis. Morphology by itself, has so far failed to give a clear picture (e.g. Lake Superior diploid vs. *D. campyloptera* of the Appalachians). Instead, the practice is to return to the morphological evidence after the cytogenetic analysis is completed. Geographical distribution is of value to delimit a sexually interbreeding natural population even though the boundary between species is often obscured by disjunct ranges such as the amazing one shown by *Polystichum scopulinum.* Also with some calcicolous species of ferns, it may well be, that distribution is limited by lack of suitable habitats e.g. some Woodsias. Cytology has been extremely useful, but it is felt that too much emphasis on the criterion of homology, when so little is known about the true nature of pairing and chiasma formation at zygotene of meiosis, is apt to lead to false conclusions. — DEPARTMENT OF BOTANY, ONTARIO AGRICULTURE COLLEGE, GUELPH, ONTARIO, CANADA.

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